

Do symbiotic polychaetes migrate from host to host?

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Abstract

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It is generally considered that symbiotic animals colonise their hosts during their early stages of development. The main goal of the present study was to assess whether post-settled stages (juvenile and adult) of the symbiotic polychaete *Paradyte crinoidicola* are able to colonise their host comatulid crinoids. We also considered possible motives for symbiont migrations based on the intraspecific traumatism, size and sex structure data, and distribution pattern of *P. crinoidicola*. To this end, field sampling and experiments with depopulated hosts of the comatulid crinoid *Himerometra robustipinna* were carried out. The infestation prevalence was 62%, each infested host harbored from 1 to 7 polychaetes, and multiple infestations with 2 or 3 polychaetes per host were common. Mean intensity was 2.1 specimens per host. The dispersion coefficient was 1.7, greater than 1, indicating the tendency to contagious distribution pattern. Male/female ratio in *P. crinoidicola* was very close to the expected 1:1 ratio. About 33 % of *P. crinoidicola* had a traumatised posterior ends, and 31% damaged and regenerated parapodia, elytra and cirri, likely attributable to intra-specific fighting. In the field experiments depopulated crinoids were rapidly colonised by symbionts. The infestation characteristics of recolonised hosts didn't differ significantly to that of the control. Mean length of polychaetes and the ratio of small polychaetes to large polychaetes were similar in the experimental series and in the control, indicating a colonisation of crinoids not only by settling larvae, but predominately by migrating post-settled juveniles and adults. The male/female ratio deviated significantly in favor of males in the experimental series, suggesting that males more than females actively migrate among hosts. Intraspecific competition and searching for mating partners are proposed as causes for host swapping in *P. crinoidicola*.

Keywords

Polychaeta, *Paradyte crinoidicola*, symbiont, traumas, sex ratio, migration, host switching, recolonisation, Comatulida, crinoids, Vietnam.

Introduction

Obligatory symbiotic animals are well adapted morphologically and behaviorally to live in close association with their hosts, while it seems likely that they are vulnerable to predators during movements between the hosts (Castro, 1978). Thus, it was considered that interactions among particular symbiotic associations are established only during close contacts between hosts, as in the case of the crab (*Liopetrolisthes mitra*) inhabited sea urchins (Thiel et al., 2003), or the polychaetes (*Histiobdella homari*) associated with lobsters (Simon, 1968). Nevertheless, host-to-host migrations suggest the existence of a free-living stage in the life-cycles of symbionts, which was already demonstrated in several species of crabs and ophiuroids (e.g. Castro, 1978; Fourgon et al., 2007; Bruyn et al., 2009). Host switching was also found in the

crinoid-associated shrimp *Synalpheus stimpsoni* (VandenSpiegel et al., 1998) and in a few species of symbiotic polychaetes (Lande and Reish, 1968; Dimock, 1974; Britayev, 1991). It was supposed that host-to-host migrations should be a rather common phenomenon in symbionts with territorial behavior (Martin and Britayev, 1998). Motives for host swapping include searching for better shelter and food supply, mating partners, and intraspecific and interspecific competition (Castro, 1978; Thiel et al., 2003). However, it is not clear whether all these motives are relevant for each particular species, or if motives differ in different species.

To verify the existence of host-to-host migrations in symbiotic polychaetes we selected the scaleworm *Paradyte crinoidicola* (Potts, 1910) as it is one of the most common symbiotic polychaetes in tropical shallow waters with evidence of territoriality (Britayev et al., 1999). This species is widely

distributed in the Indo-West Pacific and inhabits more than 30 species of shallow-water unstalked crinoids or comatulids with relatively high (14 to 48%) infestation prevalence (Zmarzly, 1984; Britayev and Antokhina, 2012).

The main goal of the present study was to assess experimentally whether post-settled juvenile and adult *P. crinoidicola* migrate from host to host. We also considered intraspecific traumatism, size and sex structure, distribution pattern of polychaetes, and based on data obtained, possible motives for the migrations of symbionts.

Material and methods

Sampling of crinoids and their symbionts, and field experiments were carried out in the outer part of Nha Trang Bay (South China Sea, South Vietnam), near eastern coast of Tre Island.

Host crinoid *Himerometra robustipinna* (Carpenter, 1881) employed in our studies is common in the Bay of Nha Trang, where it forms dense aggregations up to 10–15 individuals per m². Individuals are usually bright-red colored, which easily distinguishes them from other crinoids *in situ* (fig. 1a). *P. crinoidicola* is very abundant in the area (fig. 1b) and inhabits all the comatulids found in the Bay.

Specimens of *H. robustipinna* were hand-collected by SCUBA diving at 6–10 m depth. Individuals were gently pulled away from the substrate, and immediately placed in separate zip-lock plastic bags to avoid loss of symbionts. On the boat, crinoids were carefully checked and all visible polychaete symbionts were removed and fixed in 70% alcohol. Later in the laboratory, polychaetes were measured, sexed, and traumas recorded. Although individuals easily fragmented, body measurements are possible due to high correlation between length and width ($y = 12.88x + 0.328$, where y = length, x = width, $R^2 = 0.983$). Thus, only body width between bases of parapodia of the widest segments was measured. Sex was determined by the presence of oocytes in females, spermatids or spermatozoa in males. For that purpose, 1–2 midbody segments were placed on a slide in a drop of glycerol, covered by a coverslip, and analysed with a light microscope. Traumas to body and parapodia were recorded according to Britayev and Zamishliak (1996). Two main types of traumas were distinguished: small traumas (i.e. damaged elytra, cirri or parapodia, either lacking or being smaller than those of nearby segments as a consequence of regeneration processes, probably attributable to intra-specific aggressive behavior) (fig. 2b, d) and large traumas (primarily posterior end of body lost and regenerated, probably as a result of predators, e.g. fish and crustacean attacks) (fig. 2 c). Specimens lacking elytra, cirri, and posterior body end without traces of regeneration were not considered as traumatised.

To characterise the infestation of *H. robustipinna* by *P. crinoidicola* we determined the proportion of crinoids infested (prevalence) and the mean number of symbiont individuals per host infested (mean intensity). To determine the significance of differences in the male/female ratio and prevalence we used ϕ -test - angular Fisher transformation. To determine the significance of differences in the mean intensity and mean length we used t-test. To assess the distribution of polychaetes among hosts we employed the ratio of variance (σ^2) to mean

value (μ), σ^2/μ (coefficient of dispersion). If a population has a random distribution, this ratio is close to 1.0. If the population distribution is more uniform than random $\sigma^2/\mu < 1.0$, and if the population is distributed contagiously, $\sigma^2/\mu > 1.0$ (Zar, 1984).

For field experiments the area characterised by the presence of large boulders and rocky outcrops, which are suitable substrates for crinoids were selected. These boulders were separated from each other by coarse sand with dead shells and pebbles, which in general is an inappropriate substrate for crinoids.

The study design included three experimental series and a control. In the first two series depopulated and tagged specimens of *H. robustipinna* were placed on boulders with dense aggregation of crinoids to test whether post-settled symbionts are able to migrate among host individuals within the locality. In the third series a group of depopulated hosts was placed on the isolated boulder without further crinoids to test the influence of spatial isolation on host colonisation by symbionts.

A total of 42 crinoid individuals collected together with their symbionts served as control. In each of the three series of experiments 14 depopulated hosts were used. After a one-week exposure, all experimental hosts were collected and analysed. Crinoids were carefully checked for symbionts and symbionts themselves were processed as described above. It was assumed that all *P. crinoidicola* exceeding 5 mm in length or with developed sexual reproductive structures infesting depopulated crinoids were the result of migration events. This takes into account the size of late nectochaetae (Bhaud and Cazaux, 1987) and a few observations on the growth of post-settled scaleworms (Pernet, 2000). More details on the experimental design and area studied are described in a general paper dedicated to recolonisation of *H. robustipinna* by associated symbiotic community (Dgebuadze et al., 2012).

Results.

Infestation characteristics and traumatism in the control.

From the 42 crinoid specimens employed in the experiments we found 26 infested with *P. crinoidicola*, i.e. prevalence of 62%. Altogether 54 polychaetes were found, most (88.9%) with gametocytes in the body cavity. The mean length of the polychaetes was 9.3 mm. The ratio of small (L 4–7 mm) to large polychaetes (L 8–15 mm) was 0.3:1. Each infested host harboured from 1 to 7 polychaetes, and multiple infestations with 2 or 3 polychaetes per host were very common (Table 1). The mean intensity was 2.1 specimens per host. The dispersion coefficient was 1.7 (Table 1). Male/female ratio in *P. crinoidicola* was very close to the expected 1:1 (chi-square 0.083, $P > 0.1$).

Among *P. crinoidicola* infesting *H. robustipinna*, 33% showed “large” traumas. The proportion of animals with damaged and regenerated parapodia, elytra and cirri (small traumas) was similar with 30% (Table 1).

Recolonisation experiments

After 7 days of exposure all tagged crinoids except one from series 3 were recorded. The data revealed that depopulated crinoids were rapidly colonised by symbionts. The prevalence

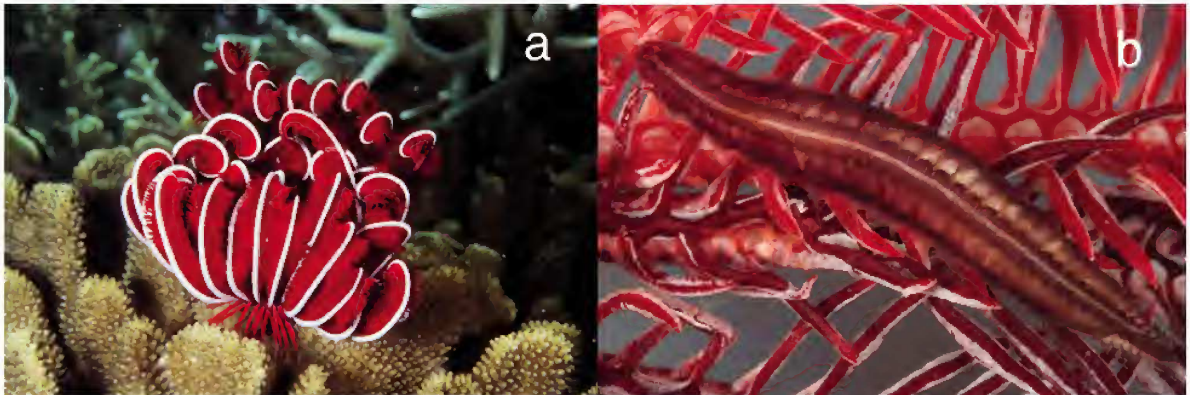


Figure 1. a. Host crinoid *Himerometra robustipinna* (Carpenter, 1881) *in situ*. b. Polychaete *Paradyte crinoidicola* (Potts, 1910) on the arm of the host.

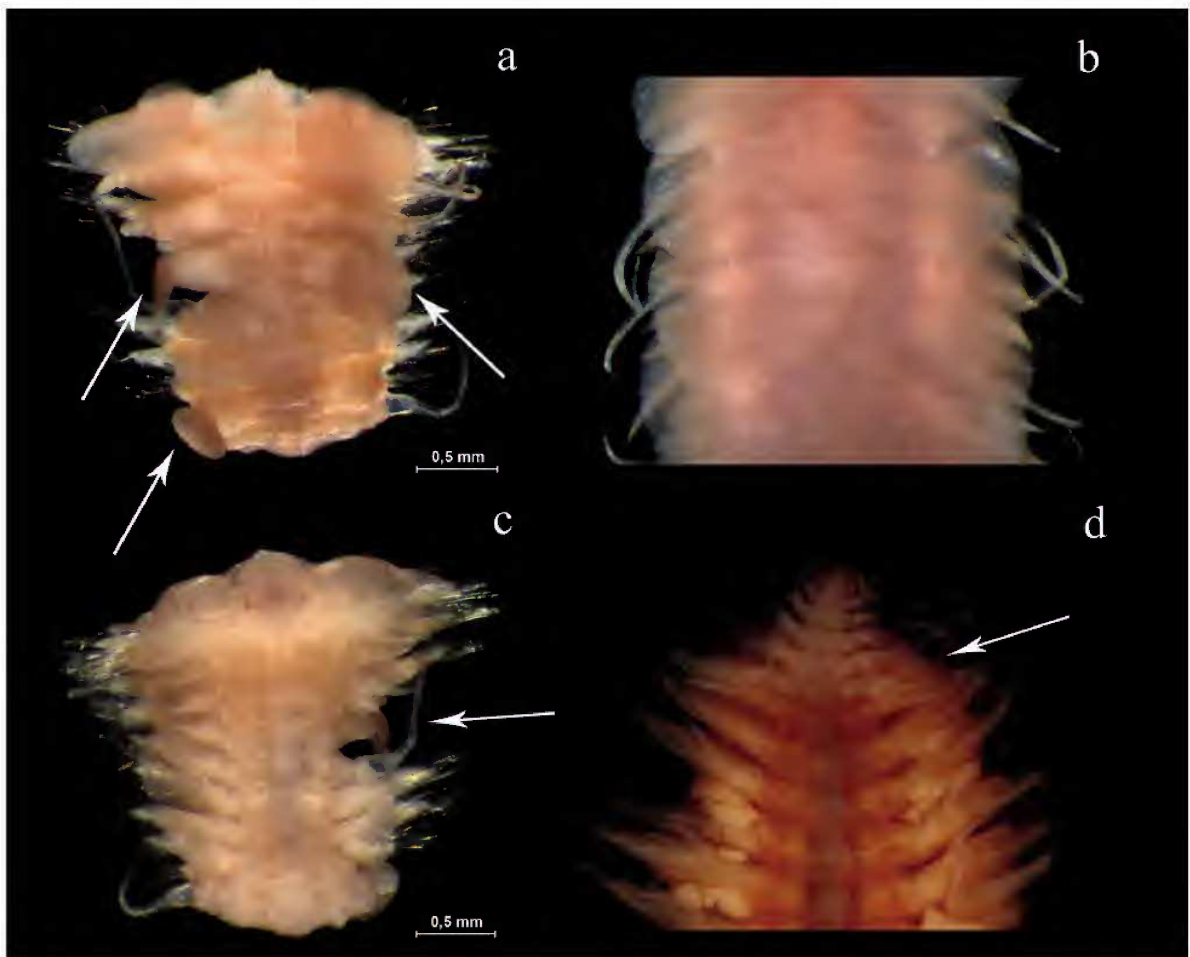


Figure 2. Traumas of *Paradyte crinoidicola*. a. Traumatized and regenerated elytra (white arrows). b. Dorsal surface of *P. crinoidicola* covered by unaffected elytra. c. Damaged and partially regenerated parapodium (white arrow). d. Traumatized and regenerated posterior end of body. White arrow indicates border between old and new chaetigers.

Table 1. Infestation characteristics, size, male/female ratio, traumas of *Paradyte crinoidicola*, and number of hosts (in parenthesis) in the control and in the experimental series.

Indices	Control (42)	Series 1 (14)	Series 2 (14)	Series 3 (13)
Symbionts number	54	13	10	24
Prevalence (infested hosts)	62% (26)	57% (8)	50% (7)	64% (8)
Mean intensity ($\pm$ SD)	2.1 ($\pm$ 1.4)	1.6 ($\pm$ 1.1)	1.4 ($\pm$ 0.5)	2.7 ($\pm$ 1.7)
Mean length. mm ($\pm$ SD)	9.3 ($\pm$ 2.9)	10.2 ($\pm$ 3)	8.9 ($\pm$ 2.1)	8.7 ($\pm$ 3.3)
Small/large worm ratio	0.3	0.2	0.2	0.3
Dispersion coefficient	1.7	1.1	0.3	4.3
Male/female ratio	1.1	1.4	3.5	5.7
Small traumas (%)	30	15	0	42
Large traumas (%)	33	38	60	29

of infestation was high and close to that in the control, while mean intensity of recolonised hosts deviated in both sides to that of the control (Table 1). The dispersion coefficient varied significantly from 0.3 in series 2 to 4.3 in series 3. This variability correlates rather with the low number of polychaetes in series 1 and 2 than with biological interactions.

Mean length of polychaetes and the ratio of small to large polychaetes were similar in the experimental series and in the control (Table 1). Male/female ratio deviated in favour of males in the experimental series (joint samples, chi-square 10.8, $P < 0.01$). This deviation was insignificant in series 1 and 2 (chi-square 0.3 and 2.8 respectively, $P > 0.1$), but increased substantially in the spatially isolated locations in series 3 (Table 1, chi-square 9.8, $P < 0.01$). The proportion of traumatised polychaetes varied for specimens with small traumas from 0 to 42%, and for specimens with large traumas from 29 to 60 (Table 1).

Discussion

Paradyte crinoidicola are very fragile animals, which easily fragment when disturbed and lose elytra and cirri, both original and regenerated. Thus, the actual number of animals with both types of traumas should be higher than observed, and for this particular species of scaleworm traumas of parapodia are the most relevant mark of intraspecific interactions. The high frequency of traumas similar to that in other symbiotic scaleworms with intraspecific competition for the host territory, viz. *Arctonoe vittata*, *Gastrolepidia clavigera*, *Branchipolynoe seepensis* (Britayev, 1991; Britayev and Zamyshliak, 1996; Britayev et al., 2007), suggests territoriality also in *P. crinoidicola*. On the other hand, our observations on host infestation and tendency to contagious distribution of polychaetes among hosts (the dispersion coefficient higher than 1 in the control and series 3, Table 1), disagree with the expected regular distribution in species with territorial behavior (e.g. Odum, 1971) and data on solitary distribution of *P. crinoidicola* among comatulid hosts in the Red Sea (Fishelson, 1985). We suggest, that this particular situation, viz. co-occurrence of contagious distribution and

territoriality, is related to several circumstances: (1) tolerance of adult and juvenile residents to recruits, already known in some other symbionts with territorial behavior, e.g. the crab *Allopetrolisthes spinifrons* (Baeza et al., 2002), (2) relatively large size of the host comatulid *H. robustipinna* and (3) its morphological complexity, providing isolated microhabitats for polychaetes. The discrepancy to Fishelson's observations is probably related to predation pressure regulating the abundance of polychaetes, which is low due to overfishing in the Bay of Nhatrang and relatively high in the Red Sea area studied by Fishelson (senior author's personal observation).

Our data revealed that depopulated crinoids were rapidly colonised by symbionts. The infestation characteristics of recolonised hosts didn't differ significantly to that of the control. To determine whether polychaetes infest host by migration of already settled juveniles and adults from neighbouring comatulids, or by settlement of larvae from the plankton, the mean length of polychaetes and proportion of adults in the control and in the experimental series were compared. Similar means of both indices support the hypothesis on migration of polychaetes between hosts.

Presently, host-swapping behavior has been documented in only 3 polychaete species, the hesionid *Ophiodromus puggetensis* (Lande and Reish, 1968), and the scaleworms *Arctonoe pulchra* and *A. vittata* (Dimock, 1974; Britayev, 1991). With *P. crinoidicola* our experiments revealed one further species with such a behavioral adaptation, suggesting it is a more common phenomenon among symbiotic polychaetes than has been considered so far, and proved indirectly a link between territoriality and host-to-host migrations (Britayev, 1991).

The experimental series 1 and 2 indicated movement of symbionts in dense host aggregations or over short distances. It has been suggested such migrations are more common between hosts with contagious distribution patterns than between spatially dispersed hosts (Thiel et al., 2003). The infestation characteristics of crinoids in the spatially isolated site (series 3) were not lower than that of crinoids from aggregations of series 1 and 2, suggesting also extensive long-distance host-to-host migrations. This unexpected result

indicates the ability of symbionts to rapidly cross inappropriate biotopes and requires special consideration.

As has been demonstrated earlier (Britayev, 1991), intraspecific aggressive interactions accompanied by traumas of body appendages lead to relocation of symbiotic polychaetes from one host to another. The high frequency of traumas in the control and series 1 and 3 indirectly indicates intraspecific interactions in *P. crinoidicola* populations, so we can suggest that one reason of their host-to-host migration is intraspecific competition. Another possible reason likely is the search for mating partners. The deviation in the sex ratio in favor of males in experimental series indicates a higher migratory activity of males in comparison to females. This latter phenomenon attributed to searching for a mate is well known in symbiotic crabs (e.g. Wirtz and Diesel, 1983; Yanagisawa and Hamaishi, 1986; Baeza, 1999; Thiel et al., 2003), but only recently documented in symbiotic polychaetes (Britayev et al., 2007).

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